Canine sexual dimorphism in *Ardipithecus ramidus* was nearly human-like

Gen Suwa[a,1,2], **Tomohiko Sasaki**[b,1], **Sileshi Semaw**[c,d], **Michael J. Rogers**[e], **Scott W. Simpson**[f], **Yutaka Kunimatsu**[g], **Masato Nakatsukasa**[h], **Reiko T. Kono**[i], **Yingqi Zhang**[j], **Yonas Beyene**[k], **Berhane Asfaw**[l], and **Tim D. White**[c,m]

[a]The University Museum, The University of Tokyo, Tokyo 113-0033, Japan; [b]The Kyoto University Museum, Kyoto University, Kyoto 606-8501, Japan; [c]Centro Nacional de Investigación sobre la Evolución Humana, 09002 Burgos, Spain; [d]Stone Age Institute, Gosport, IN 47408; [e]Department of Anthropology, Southern Connecticut State University, New Haven, CT 06515; [f]Department of Anatomy, Case Western Reserve University School of Medicine, Cleveland, OH 44106; [g]Department of Business Administration, Ryukoku University, Kyoto 612-8577, Japan; [h]Laboratory of Physical Anthropology, Kyoto University, Kyoto 606-8502, Japan; [i]Faculty of Letters, Keio University, Yokohama 223-8521, Japan; [j]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; [k]French Center for Ethiopian Studies, Addis Ababa, Ethiopia; [l]Rift Valley Research Service, Addis Ababa, Ethiopia; and [m]Department of Integrative Biology, University of California, Berkeley, CA 94720-3140

Contributed by Gen Suwa, October 23, 2021 (sent for review September 9, 2021; reviewed by Richard F. Kay and Philip Reno)

Body and canine size dimorphism in fossils inform sociobehavioral hypotheses on human evolution and have been of interest since Darwin's famous reflections on the subject. Here, we assemble a large dataset of fossil canines of the human clade, including all available *Ardipithecus ramidus* fossils recovered from the Middle Awash and Gona research areas in Ethiopia, and systematically examine canine dimorphism through evolutionary time. In particular, we apply a Bayesian probabilistic method that reduces bias when estimating weak and moderate levels of dimorphism. Our results show that *Ar. ramidus* canine dimorphism was significantly weaker than in the bonobo, the least dimorphic and behaviorally least aggressive among extant great apes. Average male-to-female size ratios of the canine in *Ar. ramidus* are estimated as 1.06 and 1.13 in the upper and lower canines, respectively, within modern human population ranges of variation. The slightly greater magnitude of canine size dimorphism in the lower than in the upper canines of *Ar. ramidus* appears to be shared with early *Australopithecus*, suggesting that male canine reduction was initially more advanced in the behaviorally important upper canine. The available fossil evidence suggests a drastic size reduction of the male canine prior to *Ar. ramidus* and the earliest known members of the human clade, with little change in canine dimorphism levels thereafter. This evolutionary pattern indicates a profound behavioral shift associated with comparatively weak levels of male aggression early in human evolution, a pattern that was subsequently shared by *Australopithecus* and *Homo*.

canine dimorphism | Bayesian estimate | *Ardipithecus ramidus* | *Australopithecus* | *Homo*

A small canine tooth with little sexual dimorphism is a well-known hallmark of the human condition. The small and relatively nonprojecting deciduous canine of the first known fossil of *Australopithecus*, the Taung child skull, was a key feature used by Raymond Dart for his inference that the fossil represented an early stage of human evolution (1). However, recovery of additional *Australopithecus* fossils led to the canine of *Australopithecus africanus* to be characterized as large (compared to that of humans or "robust australopithecines") and its morphology primitive, based on a projecting main cusp and crown structures lacking or hardly expressed in *Homo* (2). Later, the perception of a large and primitive canine was enhanced by the discovery and recognition of *Australopithecus afarensis* and *Australopithecus anamensis* (3–8), the latter species extending back in time to 4.2 million years ago (Ma). Although assessments of canine size variation and sexual dimorphism in *Au. afarensis* were hampered by limited sample sizes (9, 10), some suggested that the species had a more dimorphic canine than do humans, equivalent in degree to the bonobo (11) or to chimpanzees and orangutans (12). Initially, *Au. anamensis* was suggested to express greater canine dimorphism than did *Au. afarensis* (13, 14). However, based on a somewhat larger sample size, this is now considered to be the case with the tooth root but not necessarily its crown (15–17).

Throughout the 1990s and 2000s, a pre-*Australopithecus* record of fossils spanning >6.0 to 4.4 Ma revealed that the canines of these earlier forms did not necessarily exceed those of *Au. afarensis* or *Au. anamensis* in general size (18–28). However, all these taxa apparently possessed canine crowns on average about 30% larger than in modern humans, which makes moderately high levels of sexual dimorphism potentially possible. Canine sexual dimorphism, combined with features such as body size dimorphism, inform sociobehavioral and ecological adaptations of past and present primates, and therefore have been of considerable interest since Darwin's 1871 considerations (29–57). In particular, the relationship of canine size dimorphism (and/or male and female relative canine sizes) with reproductive strategies and aggression/competition levels in primate species have been a continued focus of interest (14, 33, 35–45, 49–56). Conspecific-directed agonistic behavior in primates related to

Significance

Humans have the proportionately smallest male canines among all anthropoids and little canine sexual dimorphism. However, the evolutionary emergence of this defining condition remains unclear because until now we have lacked a reliable method of determining dimorphism in weakly dimorphic fossil species. Using a probability-based method we recently developed, we estimated canine size dimorphism in the ~4.5 million-year-old *Ardipithecus ramidus* and found it to be weak and comparable to that of modern humans. Our analysis of >300 fossils spanning 6 million years shows that male canine size reduction occurred early in human evolution, broadly coincident with the adoption of bipedality. This suggests a profound and evolutionarily deep sociobehavioral shift that minimized male–male aggression, most likely mediated by female choice.

Author contributions: G.S., T.S., S.S., M.J.R., B.A., and T.D.W. designed research; G.S., T.S., S.S., M.J.R., S.W.S., Y.K., M.N., R.T.K., Y.Z., Y.B., B.A., and T.D.W. performed research; G.S., T.S., and T.D.W. analyzed data; and G.S., T.S., S.S., M.J.R., S.W.S., Y.K., M.N., R.T.K., Y.Z., Y.B., B.A., and T.D.W. wrote the paper.

Reviewers: R.F.K., Duke University; and P.R., Philadelphia College of Osteopathic Medicine.

The authors declare no competing interest.

[1] G.S. and T.S. contributed equally to this work.

[2] To whom correspondence may be addressed. Email: gsuwa@um.u-tokyo.ac.jp.

This article contains supporting information online at http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2116630118/-/DCSupplemental.

mate and/or resource competition can be particularly intense among males both within and between groups (14, 44, 57). It is widely recognized that a large canine functions as a weapon in intra- and intergroup incidences of occasional lethal aggression (45, 58–61), and a large, tall canine has been shown or inferred to significantly enhance male fitness (50, 56). Hence, canine size and dimorphism levels in fossil species provide otherwise unavailable insights into their adaptive strategies.

Here, we apply a recently developed method of estimating sexual size dimorphism from fossil assemblages of unknown sex compositions, the posterior density peak (pdPeak) method (62), and reexamine canine sexual dimorphism in *Ardipithecus ramidus* at ~4.5 Ma. We include newly available fossils recovered from the Middle Awash and Gona paleoanthropological research areas in the Afar Rift, Ethiopia (26, 63, 64) in order to obtain the most reliable dimorphism estimates currently possible. We apply the same method to *Australopithecus*, *Homo*, and selected fossil apes, and evaluate canine sexual dimorphism through evolutionary time.

We operationally define canine sexual dimorphism as the ratio between male and female means of basal canine crown diameters (the m/f ratio). Because the canines of *Ar. ramidus*, *Au. anamensis*, and extant and fossil apes are variably asymmetric in crown shape, we examine the maximum basal dimension of the crown. This can be either the mesiodistal crown diameter or a maximum diameter taken from the distolingual to mesiobuccal crown base (7, 27, 65). In the chronologically later *Au. afarensis* and all other species of *Australopithecus* sensu lato and *Homo*, we examine the more widely available conventional metric of buccolingual breadth, which corresponds to or approximates the maximum basal crown diameter. In anthropoid primates, canine height is more informative than basal canine diameter as a functional indicator of aggression and/or related display (14, 41–44). We therefore also examine available unworn and minimally worn fossil canines with reliable crown heights.

Estimating Canine Sexual Dimorphism, the Problem

Because the sexual identity of fossil teeth can only rarely be established by associated skeletal remains with sufficient indicators of sex, there is a long history of research on inferring dental sexual dimorphism. In anthropoid primates with strong canine sexual dimorphism, the canine can often be sexed on the basis of size and shape. However, this is not the case when dimorphism is only moderate or slight. With extant and Miocene fossil apes, Kelley (66, 67) has demonstrated that a set of morphological criteria tends to distinguish sex regardless of taxa, although boundary conditions vary by species. By this method, a clearly bimodal canine (and molar) size dimorphism was established in *Lufengpithecus*, *Griphopithecus*, and *Kenyapithecus* (68–70). In these taxa, the m/f ratios of basal canine diameters are greater than 1.4 or 1.6, values comparable to, or more dimorphic than, the most dimorphic extant great ape (*Gorilla*, with m/f ratios of ~1.4 to 1.5). A similarly large m/f ratio (>1.5) has been reported for *Nacholapithecus*, based on bimodal nonoverlapping canine size distributions (71, 72). Somewhat lower m/f ratios of 1.34 and 1.37 were reported in Late Miocene *Ouranopithecus* (73) and Pleistocene *Gigantopithecus* (74), respectively, whereas taxonomic complexities and/or smaller samples make assessments difficult in other cases (67, 72, 75–78). The m/f ratios of *Pan* and *Pongo* range from around 1.2 to 1.4, with the lowest degree of dimorphism seen in the lower canine of the bonobo (11, 15, 27, 42, 75, 79).

In anthropoid primates, including extant great apes, sexual dimorphism of the canine is generally more enhanced in the upper than in the lower canine (27, 35, 41, 42, 66). The upper canines exhibit thin enamel, especially in males (80, 81), and are sharpened distolingually by the occluding lower premolar to form a sharp distal cutting edge (80, 82–84). This morphological complex is known as the honing complex (or the C/P3 complex in catarrhines), comprising sharp upper and lower canines interlocking in occlusion along vertical wear facets/zones supported by distinct crown structures/shapes (ref. 82, see also ref. 25 pp. 212−216 and supplementary online material in ref. 27, pp. 14− 16 on hominoid canine structures and occlusal relationships). Whereas the canine is generally a conical puncturing and grasping organ in carnivores, in anthropoid primates, the upper canine functions as a sharp-edged weapon as amply inferred from wounds inflicted in physical fights (45, 58–61). In humans, the ancestral C/P3 complex is highly modified to remnant vestigial expression, and the m/f ratio of basal crown diameters varies among populations predominantly between 1.03 and 1.09 (85), although the ratio exceeds 1.1 in some modern or recent human populations (Dataset S1).)

When shape indicators of sex are unclear or not demonstrable, and when female and male canine sizes (and shape) overlap substantially, as is the case in modern humans and some nonhuman anthropoids, accurately sexing individual canines is difficult or impossible. That is, the male canine can be "feminized" as in humans, or the female canine can be large and have "male morphology" indistinguishable from those of males, as in gibbons (66, 86). However, with the expectancy that mean sizes were larger in males than in females, canine sexual dimorphism in primate fossil assemblages has been estimated by a variety of methods (9, 11, 43, 87). Here, we briefly summarize the necessary limitations inherent in these methods and then present our findings via the pdPeak method (62) that enables a more accurate and meaningful dimorphism estimate than previously possible.

Of particular interest is the timing(s) when male canine reduction occurred in the lineages leading to humans, and whether or not emergence of a human-like low level of canine size dimorphism was gradual or focused on some particular time period and circumstances.

The Mean and Binomial Dimorphism Index Methods

The most commonly applied method is known as the mean method (MM). In this method, the fossil sample is divided into two nonoverlapping subgroups by the mean, and the ratio between the larger and smaller subsample means is considered the m/f ratio (88). Although the MM has been shown to return reliable estimates of dimorphism when the m/f ratio is >1.2 or >1.3, by definition, the MM overestimates dimorphism when male and female size distributions overlap (62, 87–90). Because our goal is to ascertain the evolutionary trajectory that led to the human condition, i.e., a transition of an m/f ratio from >1.2 to < ~1.1, the MM is incapable of providing sufficient resolution. The binomial dimorphism index (BDI) (46, 91) was devised to alleviate some of the overestimating effects of the MM and other ratios such as maximum to minimum observed individuals. This is done by inputting binomial probabilities into the calculations to account for uneven sex compositions in small fossil assemblages when estimating dimorphism.

Since both MM and BDI assume that all males are larger in size than all females, these methods produce unbiased estimates of dimorphism only when the difference between sex means are greater than certain levels of within-sex variance (46, 88, and detailed in ref. 62). Strictly speaking, for an unbiased estimate to be obtained, bimodality needs to be well expressed in the combined-sex whole sample; a difference of sex means that is greater than four SD units of within-sex variance is required. However, this bias is relatively modest as long as bimodality is detectable, which corresponds to instances when sex means are separated by more than 2 SD units of within-sex variance (62). Fig. 1 depicts the degree of systematic bias inherent in the MM

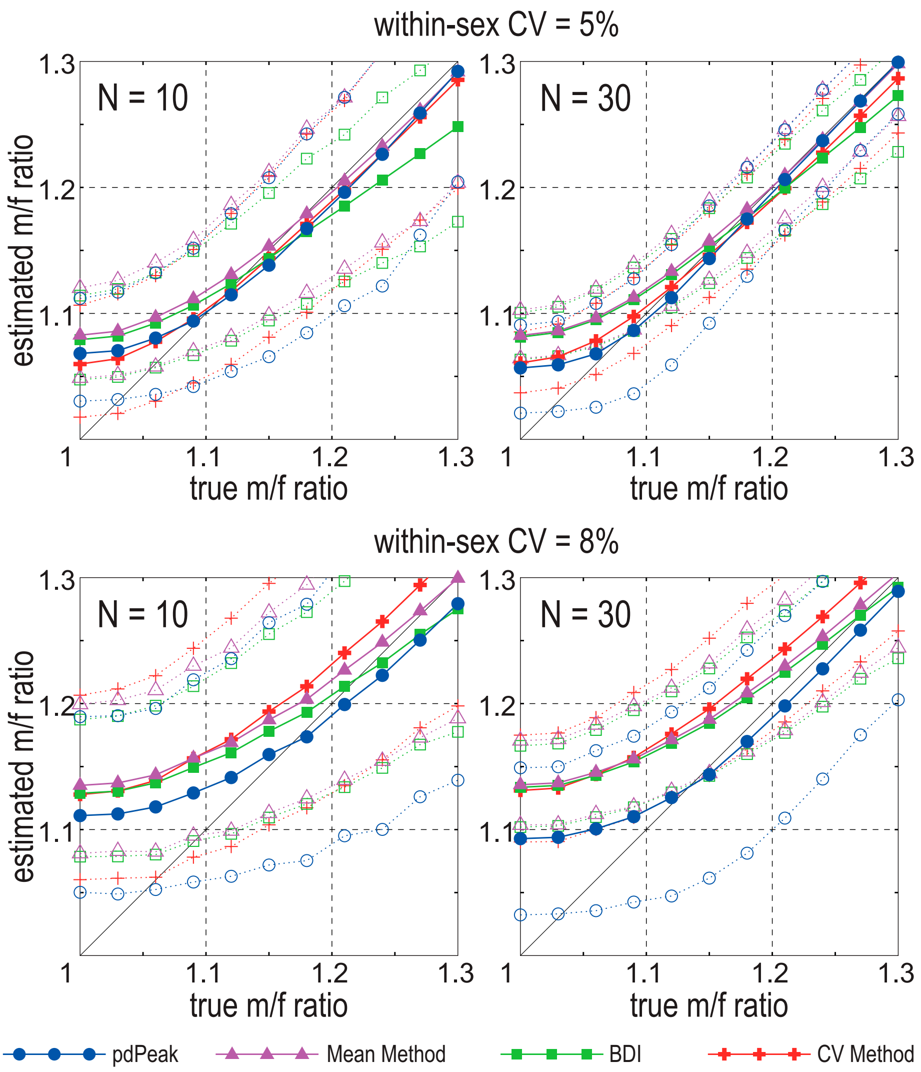

Fig. 1. Simulation tests of the pdPeak, mean, BDI, and CV methods, adapted from figure 3 in ref. 62. The *x* axis is the m/f ratio (male mean divided by the female mean) of the hypothetical populations with either a within-sex CV of 0.05 (*Upper* plots) or 0.08 (*Lower* plots). The *y* axis is the estimated population m/f ratio. Solid lines are the means, and dotted lines are the 5th (*Lower* line) and 95th (*Upper* line) percentiles of the 2,000 samples (of n = 10 or n = 30) extracted from the simulated populations. This was done for simulated populations set at m/f ratios of 0.03 intervals. pdPeak, posterior density peak; BDI, binomial dimorphism index; CV, coefficient of variation. The CV method is that of Plavcan (87). Note that unbiased m/f ratio estimates of ~1.10 and lower are possible only by the pdPeak method. The other methods systematically overestimate.

and BDI. If within-sex variation is low, for example when the within-sex coefficient of variation (wsxCV) is as low as 0.05, overestimation is slight for m/f ratios greater than 1.1. However, this is not the case when wsxCV is 0.08, a condition commonly seen in anthropoid canines including humans (Dataset S1, and figure 2 in ref. 62).

The CV Method

The widely used alternative method of assessing sexual size dimorphism in fossil assemblages is some form of the CV method (the coefficient of variation, CV, is the SD divided by the mean). It has been empirically demonstrated that the combined-sex CVs of a size dimorphic element, such as the canine of many anthropoid primates, are conspicuously elevated by the mixture of sex samples with large mean differences (9, 75, 92). Simply put, a large CV of a fossil assemblage likely indicates a large degree of sexual size dimorphism. The latter can then be estimated by regressing the m/f ratio on whole-sample (combined-sex) CV, using modern primate references of choice or comparably simulated hypothetical population sets. Such methods have been applied to the *Australopithecus* canine (11, 43), resulting in the inference that at least some *Australopithecus* species, such as *Au. afarensis* or *Au. anamensis*, had moderate dimorphism levels of canine basal crown size, as in bonobos or chimpanzees (11, 14, 43).

However, an elevated combined-sex CV can be caused either by divergent sex distributions or by high wsxCVs characteristic of the species or samples. Therefore, the validity of a CV-based estimate of sexual dimorphism is dependent entirely on the underlying within-sex variance of the sample (which is generally unknowable in fossils). Under some simplifying assumptions (equal male and female sample sizes, common within-sex CV, and a large sample size), a mathematical relationship between the m/f ratio (k), combined-sex CV (cmbCV), and wsxCV is given by the formula:

$$cmbCV = \sqrt{2[(1+k^2)/(1+k)^2](wsxCV^2+1)-1}$$

(supplementary online material and table S8 in ref. 27).

In Fig. 2, we illustrate this relationship, which shows that the CV method cannot reliably estimate population m/f ratios without

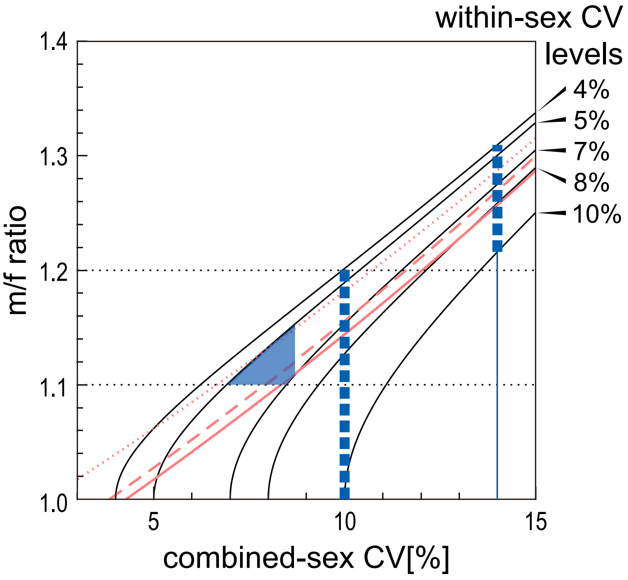

Fig. 2. Computational interrelationship of the m/f ratio, combined-sex CV, and within-sex CV. Each curvilinear line represents the relationship between the combined-sex CV (*x* axis) and m/f ratio (male mean divided by the female mean) (*y* axis) of hypothetical populations with different levels of within-sex CV. Given that anthropoid within-sex CVs of canine diameters range from <0.04 to >0.10, the *Left* and *Right* vertical interrupted lines show the possible m/f ratio ranges of a population with a combined-sex CV of 0.10 and 0.14, respectively. Note that a population with a combined-sex CV of 0.10 can represent either no dimorphism (m/f ratio of 1.0) or the lower range of an extant great ape level of dimorphism (m/f ratio of 1.2). The red lines represent alternative CV-method regression estimates of the m/f ratio. The dotted red line is the Plavcan CV method equation: $\ln Y = 2.14X - 0.047$ (87). The continuous and interrupted lines are the empirical least squares regressions of ln(m/f ratio) on combined-sex CV of the upper and lower canine maximum diameters, respectively, using the screened Plavcan dataset of anthropoids (95) (*SI Appendix*, *SI Text*). The hatched area indicates the m/f ratio range delineated by the boundary conditions assumed in Suwa et al. (table S8 in ref. 27) wherein the *Ar. ramidus* canine m/f ratio was estimated as 1.10 to 1.15, with a "best estimate" of 1.12.

a prior knowledge of wsxCV. In the case of canine dimensions, because the wsxCVs of modern human populations (Dataset S1) and geographically circumscribed populations and/or (sub)species of nonhuman anthropoids are empirically known to range from 0.04 to 0.10 (93–95), the CV method is thereby incapable of reliably estimating population m/f ratios in the <1.1 to 1.2 interval, our target of inquiry.

The Method of Moments

There have been few attempts to model sexual dimorphism by considering parameters (other than total variance) that vary according to separation of the sex means. Martin et al. (96) pointed out that the kurtosis of a mixed-sex sample changes in a predictable pattern by the magnitude of mean sex difference. The method of moments (MoM) takes a similar approach by using a formula that derives the m/f ratio from the first, second, and fourth moments (89). A combined-sex sample of a widely separated sex distribution should exhibit a "flatter" overall distribution, the opposite being the case with weak levels of dimorphism. However, when applying the MoM to actual samples, a problem occurs that the MoM cannot always calculate the m/f ratio estimate. This stems from its quartic equation that lacks real-number solutions depending on sample distribution (i.e., imaginary solutions may result). This can frequently occur when m/f ratios are low (e.g., $<\sim 1.1$). Focusing only on the real-number solutions, the MoM would tend to overestimate when wsxCV is >0.08 (albeit to a lesser extent than the MM or BDI) (*SI Appendix*, Fig. S1). Alternatively, if the imaginary solutions are considered to represent an m/f ratio of 1.0 (89), this results in an inability to distinguish between weak and no dimorphism (*SI Appendix*, Fig. S1). In a previous trial application to primate body mass data (97), the MoM was found to perform no better than the MM.

The pdPeak Method and *Ar. ramidus* Canine Sexual Dimorphism

The pdPeak method is a Bayesian-based method that in part solves the above problems (*Materials and Methods*) (62). The pdPeak method is similar to the MoM in modeling a mixture of two normal distributions of equal within-sex variance. However, instead of solving a formula from observed parameters, in the pdPeak method, population sex means and variance are estimated based on likelihoods of the observed fossil distributions. After extensive validation on both simulated and known-sex extant anthropoid datasets (62), we applied this method to the *Ar. ramidus* fossil assemblage of 13 upper canines and 11 lower canines (the latter also reported in ref. 62) and to a range of fossil apes, *Australopithecus* and *Homo*. Fig. 1 shows that the pdPeak method is capable of documenting m/f ratios of ~ 1.1 if sample size is large ($n \geq 30$) and/or the within-sex variance is low.

The results of the pdPeak method can be expressed in the form of an m/f ratio vs. wsxCV bivariate posterior distribution plot (Fig. 3) or as a male mean vs. female mean bivariate plot (*SI Appendix*, Fig. S2). We consider the pdPeak of the marginal distributions to be the best estimator of each parameter. The pdPeak estimates of the *Ar. ramidus* upper and lower canine m/f ratios were 1.06 and 1.13, respectively. This is within the modern human range of variation of population m/f ratios (Dataset S1). An important feature of the pdPeak method is that statistical probabilities of the estimates can be reliably evaluated by the Bayesian inference credible intervals. The *Ar. ramidus* upper canine m/f ratio is <1.09 at $P = 0.68$ and lies well within the modern human range of variation. The probability of the *Ar. ramidus* upper canine being at least as dimorphic as that of the least dimorphic extant great ape (the bonobo lower canine with a m/f ratio of 1.19) is $P = 0.012$. The same probability of the *Ar. ramidus* lower canine is $P = 0.068$. Thus, we can safely conclude that canine size dimorphism was weaker in *Ar. ramidus* than in any extant great ape and indistinguishable or close to the modern human condition.

The pdPeak estimates of the *Ar. ramidus* m/f ratio are accompanied by wsxCV estimates of 0.054 and 0.065 for the upper and lower canines, respectively. Because of the suggested low wsxCV, the MM and BDI estimates are also low (1.10 and 1.09, respectively in the upper canine), a further indication of the low dimorphism level of the *Ar. ramidus* canine. Previously, assuming a low wsxCV of 0.05 to 0.07, we had estimated its canine m/f ratio as between 1.10 and 1.15 with a best estimate of 1.12 (27) (Fig. 2). These previous findings are in accord with our pdPeak estimates.

As briefly noted above, an important capacity of the pdPeak method is its ability to simultaneously estimate both m/f ratio and within-sex variance. Therefore, fossil assemblages with a high whole-sample CV can nevertheless return a low m/f ratio because of a high wsxCV, depending on the actual within-sample distribution. Furthermore, this is the case regardless of the source of the elevated sample variance; i.e., a high wsxCV can stem from factors other than inherent variance of the population. For example, the often-discussed effects of time averaging that may occur in fossil assemblages are at least in part considered by the pdPeak method. This is shown in *SI Appendix*, Fig. S3.

Canine Sexual Dimorphism in Human Evolution

We applied the pdPeak method to selected fossil apes and to Pliocene and Pleistocene *Australopithecus* and *Homo* (Fig. 4,

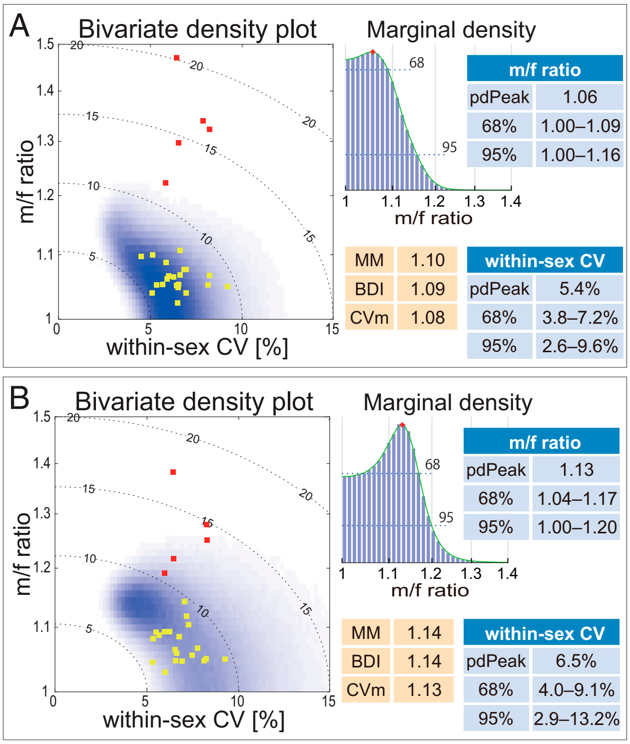

Fig. 3. *Ar. ramidus* canine sexual dimorphism. The bivariate probability distributions of within-sex CV (x axis) and the m/f ratio (male mean divided by the female mean) (y axis) are shown in gray scale. (*A*) Upper canine maximum diameter, (*B*) lower canine maximum diameter (modified from figure 6 in ref. 62). The probability densities were obtained in log scale (log-transformed data), and the axis labels were back transformed to original scale (see ref. 62 for details). Yellow and red squares, respectively, are the modern human (Dataset S1, $n \geq 20$) and extant great ape (27) population or species/subspecies values. The dotted contour lines indicate combined-sex CV levels. The marginal probability densities (based on MCMC histograms) of the logarithm of m/f ratio are shown to the *Right* of the bivariate density plots. The pdPeak values and credible intervals are shown, as well as the m/f ratio estimates of the MM, BDI, and CV (87) methods. The pdPeak m/f ratio estimate of the $n = 13$ upper canine sample is 1.06, with a 95% highest density credible interval of 1.00 to 1.16. This indicates a 0.95 probability that the population m/f ratio is 1.16 or lower. In addition, it is possible to derive bootstrap confidence intervals (CIs) of the pdPeak estimate. Bootstrap CIs represent reproducibility of the estimate given the sample distribution in hand, but, in contradistinction to the credible interval, do not provide probabilities in relation to the population value. Based on 1,000 random iterations with replacement on the $n = 13$ upper canine sample, the bootstrap pdPeak m/f ratio average is 1.08 with a 95% CI of 1.02 to 1.16. Although this additionally confirms the reliability of the pdPeak estimate, the bootstrap CI represents the probable range of the estimate and not of the population value. With the lower canine sample ($n = 11$), the pdPeak m/f ratio estimate and its bootstrap average are both 1.13, with a bootstrap 95% CI of 1.05 to 1.19, subsumed within the 95% credible interval of 1.00 to 1.20. These examples show that the Bayesian credible interval of the pdPeak m/f ratio is (generally) more conservative than the bootstrap CI (see also ref. 62).

SI Appendix, Figs. S4–S11, Dataset S2, and see also *SI Appendix*, Figs. S12 and S13 for extant great ape sample tests). *Nacholapithecus kerioi* is characterized by a high level of canine size dimorphism with clear bimodal distributions (71, 72) (*SI Appendix*, Fig. S9*B*). Near identical m/f ratios of ∼1.5 were obtained either by the pdPeak or MM methods, and slight underestimations by the BDI method, all as expected (Fig. 1). Despite the small sample size, *Hispanopithecus laietanus* (*SI Appendix*, Fig. S10*A*) likewise suggests a comparably large degree of canine dimorphism. We also examined three fossil apes (*SI Appendix*, Figs. S10*B* and S11), *Ouranopithecus macedoniensis, Oreopithecus bambolii*, and *Gigantopithecus blacki*, considered by some to exhibit a reduced canine or C/P3 complex convergent on the human clade. In all three taxa, strong dimorphisms broadly equivalent to the chimpanzee or orangutan conditions are indicated. The 25 upper canines of *G. blacki* returned a pdPeak m/f ratio of 1.37 (>1.28 at $P = 0.95$), conclusively as dimorphic as in chimpanzees or orangutans. *O. macedoniensis* also shows a broadly comparable level of dimorphism with a lower canine pdPeak m/f ratio of 1.32, although uncertainty is greater because of smaller sample sizes.

We next examined the post-*Ar. ramidus* taxa/populations of the human clade (Fig. 4 and *SI Appendix*, Figs. S5–S9*A*). It can be seen that canine dimorphism was weak and approximated the modern human condition not only in *Ar. ramidus* but also throughout human evolution in high probability. *Au. anamensis* and *Au. afarensis* (either whole species samples or their subsets, see Dataset S2) tend to have mandibular canines with high combined-sex CVs of >0.10, resulting in high m/f ratios of ∼1.2 by the MM, BDI, or CV methods, concordant with previous reports (11, 43). However, the pdPeak method shows that the large variation is explained by a high wsxCV of ∼0.09 to ∼0.10 and m/f ratios not significantly greater than 1.10. Thus, *Au. anamensis* and *Au. afarensis* canine dimorphism was probably weaker than in bonobos, and consistent with a low level of canine dimorphism inferred for the chronologically earlier sister taxon *Ar. ramidus*.

In *Australopithecus* and *Homo*, some of the species/populations are represented by relatively larger samples, enabling results that are statistically well constrained. For *Australopithecus*, the largest samples occur in *Au. africanus* (lower canine $n = 28$) and *Australopithecus robustus* (upper canine $n = 29$) (*SI Appendix*, Fig. S6). The pdPeak dimorphism of the *Au. africanus* lower canine is 1.09, with an m/f ratio <1.11 at $P = 0.68$ and <1.15 at $P = 0.95$. With the *Au. robustus* upper canine, the pdPeak m/f ratio is 1.11 (<1.14 at $P = 0.68$, and <1.17 at $P = 0.95$). This suggests that sexual dimorphism in *Australopithecus* was close to the modern human condition regardless of differences in absolute and relative crown sizes and crown morphologies.

The Early Pleistocene record of *Homo* is too scant to make detailed assessments, but the Middle Pleistocene Atapuerca Sima de los Huesos (SH) population sample is instructive. Previous evaluations suggested a canine size dimorphism slightly greater than in modern humans, via a whole-sample (combined-sex) CV of ∼0.08, perhaps with an m/f ratio as large as 1.15; the latter was inferred from associations with morphologically sexed mandibles (98). To the contrary, the currently available Atapuerca SH upper canine sample of $n = 23$ (99) returns a pdPeak m/f ratio of 1.09 (<1.12 at $P = 0.95$) (*SI Appendix*, Fig. S8*A*), well within the modern human range. This is concordant with a recent dimorphism assessment of the SH sample on canine tissue attributes (enamel and dentine volumes and surface areas) that concluded that sexual dimorphism did not exceed that of modern humans (100). The *Homo neanderthalensis* canine sample of the present study exhibits an upper canine ($n = 25$) pdPeak m/f ratio of 1.12 (<1.16 at $P = 0.95$), also only marginally greater than in modern humans (*SI Appendix*, Fig. S8*B*). Finally, the European Upper Paleolithic sample of sexed individuals (101) returns pdPeak m/f ratios of 1.09 in both upper and lower canines, corresponding to the modern human condition; the latter pdPeak estimates compare with m/f ratios of 1.08 and 1.05 for the upper and lower canines, respectively, based on sex assignments via their associated pelves.

Discussion

Taken together, our results suggest that a greatly reduced, weak canine dimorphism characterized the early members of the human clade. Our pdPeak estimates and probabilities indicate that canine

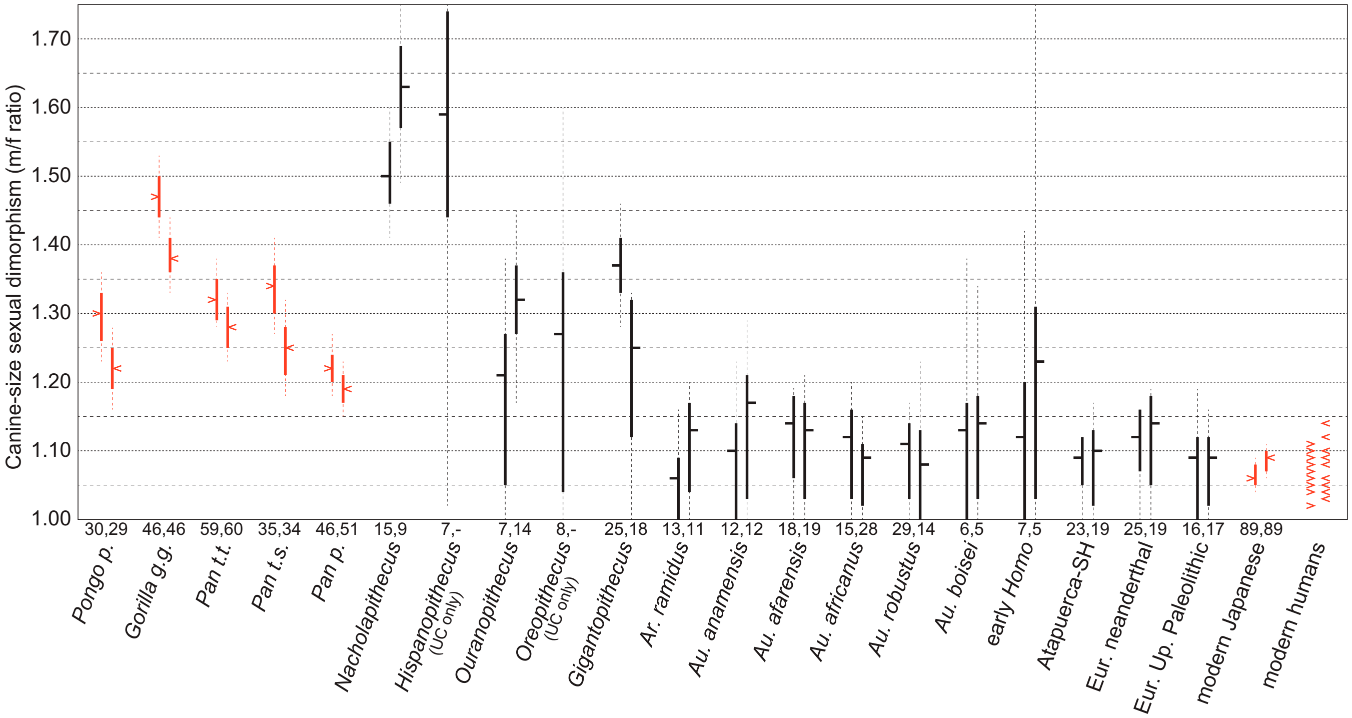

Fig. 4. Canine sexual dimorphism in fossil apes, *Ar. ramidus*, *Australopithecus*, and *Homo*. The m/f ratios (male mean divided by the female mean) of the fossil samples estimated by the pdPeak method are shown (in black) and compared to the actual population m/f ratios of the extant great apes and modern humans (in red). The Bayesian credible intervals of the pdPeak estimates provide reliable probable ranges of the actual population values (see ref. 62), and therefore the pdPeak mf/ratios and credible intervals are compared to the extant sample values and CIs. In black, the pdPeak m/f ratio estimate is shown by the horizontal tick, and the solid and dashed vertical lines indicate the 68% and 95% credible intervals, respectively. In red, the sample m/f ratio is shown by the horizontal arrowhead, and the solid and dashed vertical lines indicate the 68% and 95% CIs, respectively. For each taxon/population, upper canine on the *Left*, lower canine on the *Right*, sample sizes are indicated below the vertical lines. Note that the high m/f ratio obtained for the lower canine of early *Homo* is based on a small sample size of five. See *SI Appendix*, Figs. S4–S11 for a fuller presentation of the pdPeak results of each taxon/population. The extant great ape and modern Japanese samples are from Suwa et al. (27) and Sasaki et al. (62) and the other modern humans were taken from Dataset S1. The latter are based on population means available in the literature and shown as point values with the red arrowheads. *P. t. t.*, *P. t. s.*, and *P. p.* are *Pan troglodytes troglodytes*, *P. t. schweinfurthi*, and *P. paniscus*, respectively. See *SI Appendix*, Figs. S12 and S13 for test applications of the pdPeak method on the extant samples and how the pdPeak estimates relate to actual sample values and CIs and in relation to sample size. The latter results show that both uncertainty and overestimation bias at low levels of dimorphism become greater with smaller sample sizes and larger within-sex variance (as in the simulation results of Fig. 1), and that a modern human level of dimorphism of <1.10 would tend to be overestimated to an m/f ratio of generally 1.1 to 1.2 if within-sex variance was large (as estimated for some of the *Australopithecus* samples, see section *Canine Sexual Dimorphism in Human Evolution* above).

size dimorphism was close to the modern human condition as early as in *Ar. ramidus* at ∼4.5 Ma. Despite the considerable size variation seen in early *Australopithecus* canines, by concurrently modeling within-sex variance, it now appears that dimorphism levels of early *Australopithecus* were likely as low as in *Ar. ramidus*. The slightly greater pdPeak estimates of the m/f ratio in *Au. anamensis* and *Au. afarensis* can be inferred to reflect a combination of sample bias, elevations of variance from mixing populations, and/or fluctuations within a common weak level of canine size dimorphism close to or only slightly greater than in modern humans. Because tooth crown size can covary with body size in mix-sexed samples (102), body size variation/dimorphism may also be a contributing factor to differences in canine size dimorphism levels. We await future fossil finds to test whether or not subtle differences in canine dimorphism occurred among Pliocene *Australopithecus* species and populations. We note that considerable population variation is seen in the m/f ratios of modern humans (Dataset S1).

In *Ar. ramidus*, and in early *Australopithecus* species, size dimorphism of the lower canine crown tends to be greater than that of the upper canine (but not in *Au. africanus* and *Au. robustus*). Although statistical uncertainties preclude a definitive conclusion, this may reflect how the C/P3 complex was modified early in human evolution, as inferred from *Ar. ramidus* (27). Assuming an ancestral C/P3 honing complex, the *Ar. ramidus* upper canine appears morphologically more derived than the lower canine. We previously interpreted this as selection having operated more strongly on the behaviorally important male upper canine, whereas morphological change in the lower canine could have lagged behind (25, 27, 65). That the m/f ratio pdPeak estimates are lower in the upper canines of *Ar. ramidus*, and perhaps also in early *Australopithecus*, supports this interpretation. This is contrary to the greater size dimorphism generally observed in the upper compared to lower canines in extant great apes and other anthropoids with significant degrees of canine sexual dimorphism (42, 43).

It is well known that canine crown height is more closely related to behavioral aggression and/or competition levels than is basal crown size (41, 43, 44, 103). This is clearly expressed metrically in the canines of anthropoids in which crown height dimorphism is considerably enhanced over basal crown diameter dimorphism (*SI Appendix*, Fig. S14 and Dataset S3). Some anthropoids (colobines and *Ateles*) exhibit only weak basal crown dimorphism (<1.2) but large degrees of height dimorphism (>1.5) (42, 43) (*SI Appendix*, Fig. S14), indicating that the latter is the selectively more crucial. In extant great apes, canine dimorphism in crown height is greater than in basal diameters, albeit to a lesser extent than in Old World monkeys.

This is associated with a proportionately higher crowned canine in males, although overlap in relative heights occurs between sexes particularly in *Pan* (27, 66). The taller canine crown in males is attained predominantly by a prolonged growth period in apes (104) and in cercopithecids (105), and has been demonstrated to impact male reproductive success (50, 56).

From the foregoing, as previously noted (16, 27, 103), it is necessary to examine canine crown height and its dimorphism in *Ar. ramidus* and the other species. In the fossil record, however, reliable evaluation of unworn crown height is greatly constrained by the shortage of fully developed canine crowns lacking substantial wear and/or damage. We therefore followed Kelley (66) in compensating small amounts of cusp tip loss (<1~2 mm), and assessed crown heights in six available *Ar. ramidus* upper canines (Dataset S4). Although small sample size precludes a statistically robust estimation, the pdPeak estimate of *Ar. ramidus* canine crown height m/f ratio is 1.10 (<1.14 at $P = 0.95$). The short crown heights of the probable males attest to the advanced "feminization" of the *Ar. ramidus* canine (Fig. 5), resulting in low sexual dimorphism in both basal crown diameter and crown height.

Although weak or minimal canine dimorphisms occur in some nonhuman anthropoids (42, 43) (*SI Appendix*, Fig. S14), this is variably attained. Some taxa are characterized by females with large canines (hylobatids and some pitheciines), while others exhibit some combination of a moderately large female canine and a relatively small but still projecting male canine (callithrichids and *Aotus*) (Fig. 6 and Dataset S3). The canines of these taxa potentially function as weapons in territorial and/or mate competition in both sexes (see ref. 55 on competition/aggression in monogamous *Aotus*). The extreme degree of male canine reduction seen in the weakly dimorphic *Ar. ramidus* is unknown in nonhuman anthropoids with the exception of perhaps *Callicebus* and *Brachyteles* (Fig. 6) (33, 43, 44, 106–109).

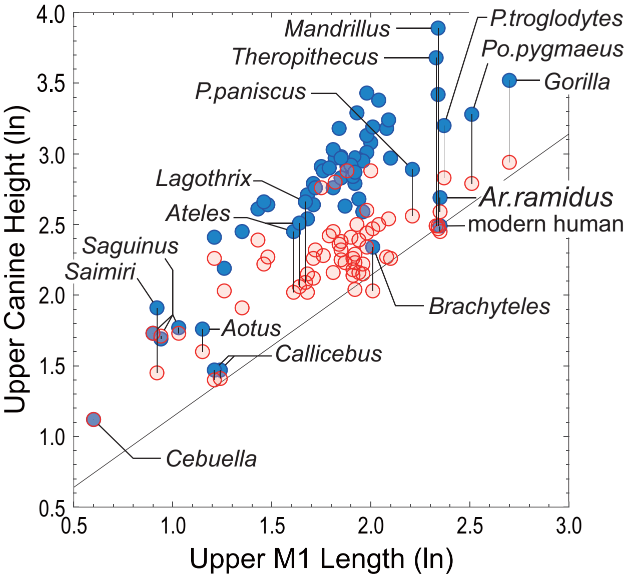

Fig. 6. Upper canine crown height of *Ar. ramidus* compared with that of extant anthropoids. Mean labial crown height (*y* axis) plotted against mean upper first molar (M1) lengths (*x* axis), both in log scale. Each data point represents species and sex means: male (blue circle), female (red circle). Mean M1 lengths are combined sex so that both male and female canines can be compared in the same relative scale and because it is difficult to segregate sex in fossil taxa. The diagonal line indicates isometry passing through the mean of modern *H. sapiens* males (modern Japanese). The plotted data are shown in Dataset S3, and based on Suwa et al. (27) and a conservatively screened version of the Plavcan dataset (95) (*SI Appendix*, *SI Text*).

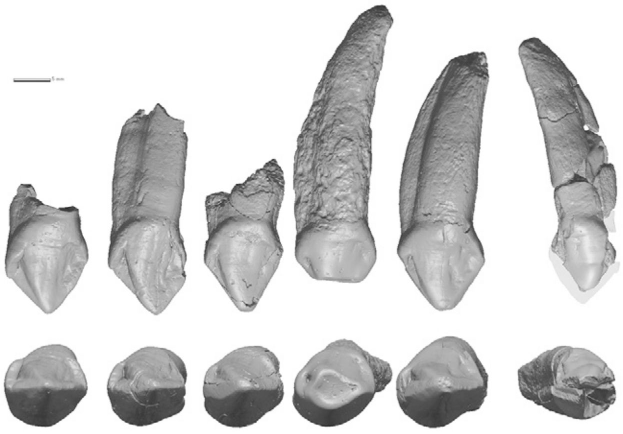

Fig. 5. *Ar. ramidus* upper (maxillary) canine variation. Relatively well-preserved *Ar. ramidus* upper (maxillary) canines from the Middle Awash research area, Afar Rift, Ethiopia, demonstrate low crown height and weak sexual dimorphism. From *Left* to *Right*, *Top* row lingual and *Bottom* row occlusal views of ARA-VP-6/1 (*Left* reversed), ARA-VP-1/300 (*Right*), ARA-VP-1/3429 (*Left* reversed), SAG-VP-7/118 (*Left* reversed), ARA-VP-1/1818 (*Right*), and ARA-VP-6/500 *Left*. The five specimens on the *Left* are probable males, and the *Far Right* specimen, ARA-VP-6/500, a female. The ARA-VP-6/500 canine does not preserve the apical crown (translucent portion hypothetical), but its crown height was reasonably estimated (*SI Appendix*, Fig. S15). The well-worn SAG-VP-7/118 canine is included as an example of apical wear ubiquitous in known *Ar. ramidus* upper canines and to show variation in shoulder heights and occlusal view crown shape. Mesial shoulder is high in ARA-VP-6/1, and low in SAG-VP-7/118 and ARA-VP-1/1818. In occlusal view, SAG-VP-7/118 and ARA-VP-1/300 are mesiodistally longer than buccolingually broad, whereas the other specimens are subequal in mesiodistal and buccolingual diameters (65). Note that all specimens exhibit a well-developed, voluminous mesiolingual ridge demarking a deep cleft-like mesiolingual groove. This structural pattern is best considered close to that of an ancestral honing C/P3 complex and is morphologically more primitive than in known examples of early *Australopithecus* (27).

Relative to molar size, *Ar. ramidus* male upper canine height is decidedly shorter than in male *Pan paniscus* (bonobo), and broadly comparable to female extant great apes (and other female anthropoids) and male *Brachyteles* (Fig. 6). *Brachyteles* forms a male philopatric multimale/multifemale society with a polygynandrous reproductive strategy, and is known for their extreme intermale tolerance and weak aggression in competing for sexual access to receptive females (110, 111). Strier (110) considered male–female codominance as a key factor of this behavioral condition (see also ref. 112 regarding bonobos). This compares with *Ateles* characterized by male dominance over females and greater intra- and intergroup aggression than in *Brachyteles*, despite a generally low level of intragroup male–male aggression and a strong female choice component as in the other atelins (111, 113). *Lagothrix* is also known by male philopatry, polygynandry, and generally tolerant intermale relationships (111), but nevertheless exhibits large male canines (42, 106), moderate body size dimorphisms (114, 115), and male dominance over females (116). It is tempting to speculate that the *Ar. ramidus* condition was a part of a sociobehavioral complex that involved a strong inclination for male–female codominance. Under such sociobehavioral conditions, a less projecting and less dagger-like male canine could have evolved via selection mediated by female mate preference, as previously suggested (27, 51).

The available evidence of basal canine crown diameter and crown height is summarized in Fig. 7 spanning >6 million years. Although data are scarce before ~4.5 Ma, there are now nine canines known from the 5- to 7-Ma time period attributed to *Orrorin tugenensis* (20, 21), *Ardipithecus kadabba* (19, 24, 25, 28),

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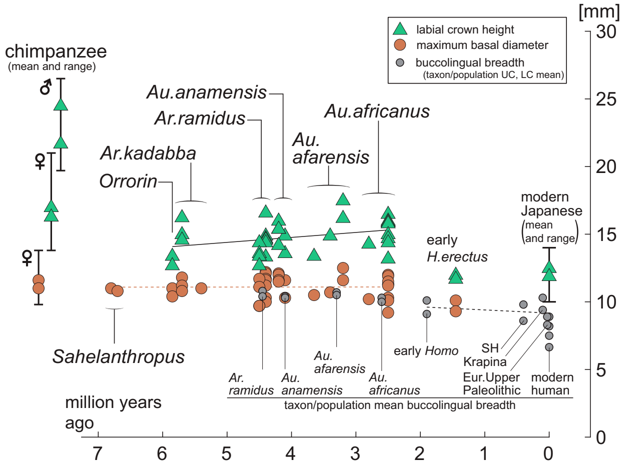

Fig. 7. Canine crown height through time. Canine size of individual specimens with unworn crown heights are plotted: green triangles, labial height; orange circles, maximum basal diameter. Given the small sample sizes of unworn/minimally worn canines, the upper and lower canines are combined. Sample sizes are: *O. tugenensis* (n = 2), *Ar. kadabba* (n = 3, including two rough height estimates), *Ar. ramidus* (n = 11), *Au. anamensis* (n = 6), *Au. afarensis* (n = 4, including one rough height estimate), *Au. africanus* (n = 10), and *Homo erectus* (n = 2). The rough crown height estimates are included to indicate possible ranges. Two *Sahelanthropus* and one *Ar. kadabba* canine without crown heights are plotted. Specimen specifics are shown in Dataset S4. The gray circles are the upper and lower canine taxon/population means of buccolingual breadths (in each circle pair, the upper canine breadth is the larger). For scale, *Pan troglodytes* and modern human unworn canine crown heights (vertical line and green triangles), maximum diameters (vertical line and orange circles) and buccolingual breadths (gray circles) are shown at the *Far Left* and *Right*, respectively (symbol pairs are upper and lower canine means). Modern human mean buccolingual breadths are the maximum and minimum population means (of both upper and lower canines) of Dataset S1; the *Upper* two circles represent an Australian aborigine sample, and the *Lower* two circles are from a San sample. Solid and interrupted lines are the least squares best fit lines of individual crown height (black), individual maximum diameters (orange), and taxon/population mean buccolingual diameters (gray), respectively. With the current small samples, there are little apparent size changes between >6 Ma and ∼3 Ma. A slight reduction in canine size (basal diameter and height) occurred in *Homo* after ∼2.5 Ma.

and *Sahelanthropus tchadensis* (22, 23). All are broadly equivalent to the canines of extant female chimpanzees in basal crown dimensions, but tend to be lower crowned. They are within the size range of *Ar. ramidus* and early *Australopithecus* canines, strongly suggesting that male canine reduction was already attained in these Late Miocene taxa.

At ∼4.5 Ma, canine sexual size dimorphism in *Ar. ramidus* was unambiguously weaker than in all extant great apes, including the least dimorphic bonobo. The *Ar. ramidus* dimorphism level was probably within or close to the modern human ranges of population variation. However, this seems to be the case more securely for the upper canines, whereas dimorphism in the lower canines may have remained somewhat greater. Canine sexual dimorphism in *Australopithecus* can be summarized as broadly equivalent to the *Ar. ramidus* condition, although it is possible that dimorphism levels in some species/populations were slightly higher. During the Pleistocene, a slight decrease of absolute canine size apparently occurred through time, together with crown structure simplification or modification, leading to the modern human condition. It is possible that this was accompanied by a slight decrease of size dimorphism, especially among lower canines. However, with the currently available fossil sample sizes, it is not possible to objectively assess the subtleties of such evolutionary trajectories. At the cruder scale of the available evidence, a drastic reduction of male canine size and projection can be hypothesized to have occurred early in human evolution, establishing minimal canine dimorphism deep in evolutionary time. Only minor perturbations in dimorphism levels occurred thereafter.

Our results considerably strengthen the idea that male canine reduction occurred very early in human evolution and broadly coincident with the adoption of bipedality (best exemplified by *Ar. ramidus*) (63, 65). Because *Ar. ramidus* and earlier fossils attributed to the human clade lack noticeable indications of postcanine expansion or enhanced mastication (18–28, 117), both classic and newer ideas (31, 34, 118) that attempted to explain initial canine reduction via tradeoffs with masticatory function are now rejected. Another long-standing explanation for canine reduction is tool use supplanting the canine as weapons in an increasingly open environment (29, 119). This notion, going back to Darwin (reviewed in ref. 120), is effectively negated by the observation that niche expansion into open habitats occurred largely after ∼4 Ma (63, 65, 121) and that complex tool technology beyond that known in nonhuman primates is routinely seen only after ∼2.5 Ma (122, 123), although the extent of organic tool use cannot generally be assessed in the fossil record.

Because relative canine size covaries with aggression and/or competition levels related with mate and/or resource acquisition among anthropoids, the canine evidence (feminized male canine shape and minimal size dimorphism) suggests a profound behavioral shift early in human evolution, and one precipitously characterized by comparatively weak levels of male–male aggression. A reduced general level of aggression can be considered an important evolutionary prerequisite for the later acquisition of enhanced interindividual cooperation and complex prosociality, attributes that are the hallmarks of our lineage (e.g., refs. 124, 125).

Materials and Methods

Datasets. The fossil samples used in the present study are summarized in *SI Appendix*, Table S1. Many of the data are in common with previous work on *Ar. ramidus* fossils from the Middle Awash (27, 65) and Gona (26) study areas in Ethiopia. Twenty-four *Ar. ramidus* canines from 22 individuals are included in our metric analysis. Basal crown dimensions of eight *Ar. ramidus* canines are newly reported (five from Gona and three from the Middle Awash). All specimens and metrics are listed in Dataset S2 (basal crown diameters) and/or Dataset S4 (crown heights).

Metrics of a total of 170 *Australopithecus* and early *Homo* canines, attributed to *Au. anamensis*, *Au. afarensis*, *Au. africanus*, *Au. robustus*, *Australopithecus boisei*, and early *Homo*, were used in the present study. Most of these were taken on the original fossils by the two of us (T.D.W. and G.S.), and used in previous analyses of the *Australopithecus garhi* (126), *Au. afarensis* (127), *Au. anamensis* (7), *Ar. ramidus* (27), and *Ardipithecus kadabba* (25) dentitions. To this dataset, we added the canine metrics that subsequently became available (sources cited in Dataset S2) including some from the literature ($n = 33$), in which cases, methodological comparability between studies was cross-checked as necessary. For Middle Pleistocene and later *Homo*, in order to keep interobserver error minimal, we confined our analysis to few sources, our own metrics of *H. neanderthalensis* (n = 44 by T.D.W.), the *Homo "heidelbergensis"* Atapuerca SH sample (n = 42) in Martinón-Torres et al. (99), and the European Upper Paleolithic *Homo sapiens* metrics (n = 33) of Frayer (101). We also analyzed 111 fossil ape canines from five selected species, also by confining sources predominantly to our own metrics: *N. kerioi* (Y.K./M.N.), *H. laietanus* (T.D.W./G.S.), *O. macedoniensis* (G.S.), *O. bambolii* (G.S.), and *G. blacki* (Y.Z./R.T.K.). These were taken by the present authors adhering to the same measurement protocol, with the exception of six *O. macedoniensis* metrics taken from the literature (128). All specimens, metrics, and sources are listed in Dataset S2. Where necessary, notes on taxonomic treatment are spelled out in Dataset S2.

Summary statistics of modern anthropoid (including human) canine crown dimensions were used for comparisons. The modern human sample includes the upper and lower canine metrics of 23 populations, including the modern Japanese dataset ($n = 89$) measured by ourselves and the summary metrics of 22 populations taken from the literature. The samples, metrics, and sources are listed in Dataset S1. The modern Japanese data were also used in the canine crown height comparison across anthropoids (Dataset S3). The nonhuman anthropoid data were derived from the Plavcan dataset (95), except for the extant great ape metrics, which were taken from Suwa et al. (27).

Methods. The maximum basal crown diameter and labial crown height of the canine were measured following established methods (7, 27) (*SI Appendix, SI Text*).

The pdPeak method is fully described in Sasaki et al. (62). Briefly, dimorphism is modeled by a mixture of two homoscedastic normal distributions in log scale. A balanced sex ratio in the source population (but not in the samples) is also assumed. Situations are specified by three parameters: male mean μ_m, female mean μ_f ($\mu_m \geq \mu_f$), and SD σ common to the sexes (in log scale). Assuming independent uniform prior probability distributions and independent prior probabilities of 0.5 for sexes, the Bayes theorem yields the joint posterior probability distribution of $P(\mu_m, \mu_f, \sigma, S \mid d)$, where S is a vector of sex assignments and d is a vector of the log-transformed measurements. We followed the theories and procedures of MacLachlan and Peel (129), and based our Markov chain Monte Carlo (MCMC) sampling on the Gibbs sampler algorithm (130). To evaluate the posterior probabilities of the m/f ratio and within-sex variation simultaneously, a bivariate density plot of $\mu_m - \mu_f$ (logarithm of m/f ratio) and σ was made from the MCMC samples. We obtained the marginal posterior probability distributions of $\mu_m - \mu_f$ or σ by integrating out the other from the bivariate plot and determined its point of highest density using the expectation maximization algorithm (131). Then, we back transformed the values to normal scale: to the m/f ratio by $exp\,[\mu_m - \mu_f]$ and to the within-sex CV (wsxCV) by $\sqrt{exp\,[\sigma^2] - 1}$. We term these the posterior density peak (pdPeak) estimates and consider the pdPeak value to be the single best estimator of the population m/f ratio or wsxCV. The credible intervals of Bayesian inference were also determined from the marginal posterior distributions. The credible intervals shown in Fig. 3 (and in *SI Appendix*, Figs. S4–S11 and Dataset S2) are the 95% highest posterior density intervals (HDIs), the interval(s) enclosed by points whose probability density and above integrates to 0.95, or the likewise 68% HDIs (corresponding to ±1 SD range of a normal distribution).

We assessed the performance of the pdPeak method by using simulated (computationally generated) datasets that were sampled from hypothetical populations that conform to the model assumptions. The population m/f ratios were set to vary from 1.0 to 1.3, and wsxCVs were designated as either 5% or 8% (*SI Appendix, SI Text*). Results of simulation tests on deviations from assumptions are reported in ref. 62. Such effects were found to be generally slight, with the exception of a highly unbalanced sex ratio or a situation that we term a "head-to-head skew" (negative skew in females and positive skew in males). In these cases, the pdPeak m/f ratio estimates would tend to slightly underestimate (see ref. 62). Validation analyses using the known-sex samples of a wide range of extant anthropoids are detailed in ref. 62, and those on the extant great ape and modern Japanese samples are presented in *SI Appendix*, Figs. S12 and S13. The results of these extant sample tests were found to largely parallel the results of the computationally generated simulation tests.

Data Availability. All study data are presented in the article and/or supporting information.

ACKNOWLEDGMENTS. We thank the Ministry of Culture and Tourism, the Authority for Research and Conservation of Cultural Heritage, the National Museum of Ethiopia, and the Afar Regional Government, Ethiopia, for permissions and facilitations; and the many individuals who have contributed to the recovery and study of the *Ar. ramidus* fossils. We thank the Authority for Research and Conservation of the Cultural Heritage of Ethiopia, National Museums of Kenya, Ditsong National Museum of Natural History, the Cleveland Museum of Natural History, the Royal Museum for Central Africa Tervuren, Naturalis Biodiversity Center, and B. Engesser, S. Moya-Sola, L. Rook, and G. Koufos for access and facilitation to the other materials. We thank C. Ward, J. M. Plavcan, F. Manthi, and Y. Haile-Selassie for information on *Au. anamensis* fossils, and J. M. Plavcan for the Plavcan anthropoid teeth dataset and related information (95). We thank the two reviewers for their constructive comments. This work was supported primarily by the Japan Society for the Promotion of Science (Kakenhi Grants 24000015 and 18H04007 to G.S.). Major grants for the Gona Project were made by the L. S. B. Leakey Foundation and European Union Marie Curie (FP7-PEOPLE-2011-CIG). The Late Miocene/Early Pliocene research was in part supported by the NSF (SBR-9910974 and RHOI BCS 0321893 to T.D.W. and F. C. Howell). Y.Z. has been supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant No. XDB26000000).

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